SHELL STRUCTURE OF THE SIPHONOTRETACEAN BRACHIOPODA

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ABSTRACT. The shell of the inarticulate brachiopod genera *Helmersenia*, *Multispinula*, and *Siphonotreta*, is finely banded in section with layers of apatite crystallites separated by relatively more homogeneous units presumably representing concentrations of proteinaceous derivatives. The surface texture of the protegulum and adult shell is smooth, and the most conspicuous ornamentation consists of regularly arranged prostrate spines with central canals, either communicating with the shell interior throughout life, or terminating proximally just below the external base of the spine. Consideration of the growth and distribution of spines suggests that they probably acted as protective grilles, sieving coarse particles from inhalent currents entering the commissural gape and reducing the incidence of microbenthic colonization of the shell exteriors.

A RECENT investigation of the shell surface of inarticulate brachiopods belonging to the Acrotretida showed a noteworthy differentiation in the external micro-ornamentation of certain species (Biernat and Williams 1970). In fossil and living representatives of the Craniacea and Discinacea, the surface of the first-formed shell, the protegulum, is essentially like that of the adult. Minor differences, other than the presence of growth-lines on the surface of the extra-protegular shell, do occur. Concentric ridges or lamellae may be more prominent in, or even restricted to, adult growth stages, but their development has never reflected any fundamental change in the regime of shell secretion. In all acrotretacean species examined, however, the protegulum differs significantly from the adult shell in being ornamented by closely distributed shallow pits. The pits usually fall into two distinct sizes, averaging 3 μm and 350 nm in *Torynelasma*, with the larger pits separated from one another by clusters of the smaller. The pattern is like the mould of a bubble raft and is interpreted as having been caused by deposition of calcium phosphate crystallites on the inner surface of the sealing membrane of a highly vesicular periostracum. The absence of pits from the adult part of the shell is believed to indicate the development of a strong post-protegular thickening of the inner sealing membrane which masked the vesicular topography of the rest of the periostracum.

During that investigation, the only siphonotretacean material examined consisted of *Helmersenia* and *Siphonotreta* valves dissolved out of Tremadocian cherts by hydrofluoric acid. The entire external surfaces of these shells bore densely distributed pits which were solution features although they may have included shallow depressions formed during skeletal secretion and enlarged during etching (Biernat and Williams 1970, p. 495, pl. 100, fig. 6). This possibility remained unchecked until recently when, with the ready help of Dr. L. R. M. Cocks of the British Museum, Dr. G. A. Cooper of the U.S. National Museum, and Dr. V. Y. Goryansky of Leningrad, to whom we are greatly indebted, well-preserved specimens of *Helmersenia*, *Multispinula*, and *Siphonotreta* became available for comparative study. Well-preserved shells of *Alichovia*, *Schizambon*, and *Dysoristus*, the only other genera assigned to the superfamily (Rowell *in* Williams *et al.* 1965, p. H288; Goryansky 1969, p. 97) could not be obtained. But the shell structure of *Alichovia* and *Schizambon* is unlikely to differ significantly from that

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of the closely related *Multispinula*; and although the protegular surface of *Dysoristus* still has to be examined, the absence of spines precludes consideration of the shell structure of that stock in relation to other Siphonotretacea. In fact, as will be shown below, the development of two distinct sets of spines, and not the nature of the protegulum, is the most distinctive feature of the siphonotretacean shell.

Materials and methods. The skeletal fabric of four siphonotretacean species has been examined in detail: *Helmersenia ladogensis* (Jeremejev) from the Tremadocian Pakerortskij sandstones of Staraja Ladoga and Ivanogorod in the Leningrad area; *Multispinula perspinosa* Cooper from the Caradocian Bromide limestones, Rock Crossing, Oklahoma; *Siphonotreta unguiculata* (Eichwald) from the Caradocian Kukerskij argillaceous limestones at Kerstovo and Diatlitzy near Leningrad; and *S. verrucosa* (Eichwald) from the 'Ordovician of Volkov near Leningrad' (BB 33159–33161). For the study of shell topography, 10% acetic acid was used to remove adherent rock matrix from internal and external surfaces of valves which were then washed in a weak detergent. For the preparation of sections, specimens were left in the rock and the cut surfaces were polished with tin oxide or alumina and subsequently etched in 2% EDTA for 20 min. Both sections and shell surfaces were coated with gold-palladium for study under the Cambridge Stereoscan scanning electron microscope purchased by N.E.R.C. grant GR/3/443.

THE PROTEGULUM

The protegulum, as the first-formed mineral layer simultaneously secreted over the larval mantle, is that part of the umbonal surface of each adult valve bounded by the earliest discernible growth-line. In four brachial valves of *Helmersenia ladogensis*, the subcircular protegulum averages 380 μm in length (Pl. 75, fig. 1). Dorsal protegula of *Siphonotreta unguiculata* and *Multispinula perspinosa* Cooper have comparable lengths of 450 and 400 μm respectively. These are up to three times as large as the typical acrotretacean protegulum, which is about the same order of difference as that of the absolute size of adult shells. There is, moreover, no trace of the regular pattern of shallow pits so characteristic of the Acrotretacea. Instead, the protegular surface of all three species is pock-marked with irregularly distributed depressions, up to 3 μm in diameter and usually connected to one another by anastomosing shallow grooves (Pl. 75, fig. 3). The surface may also show a fine layering exposed at different levels (Pl. 75, fig. 2). These features are clearly solution phenomena differentially etched, during recovery of the valves from rock matrix, out of well segregated mineral layers which cannot be much

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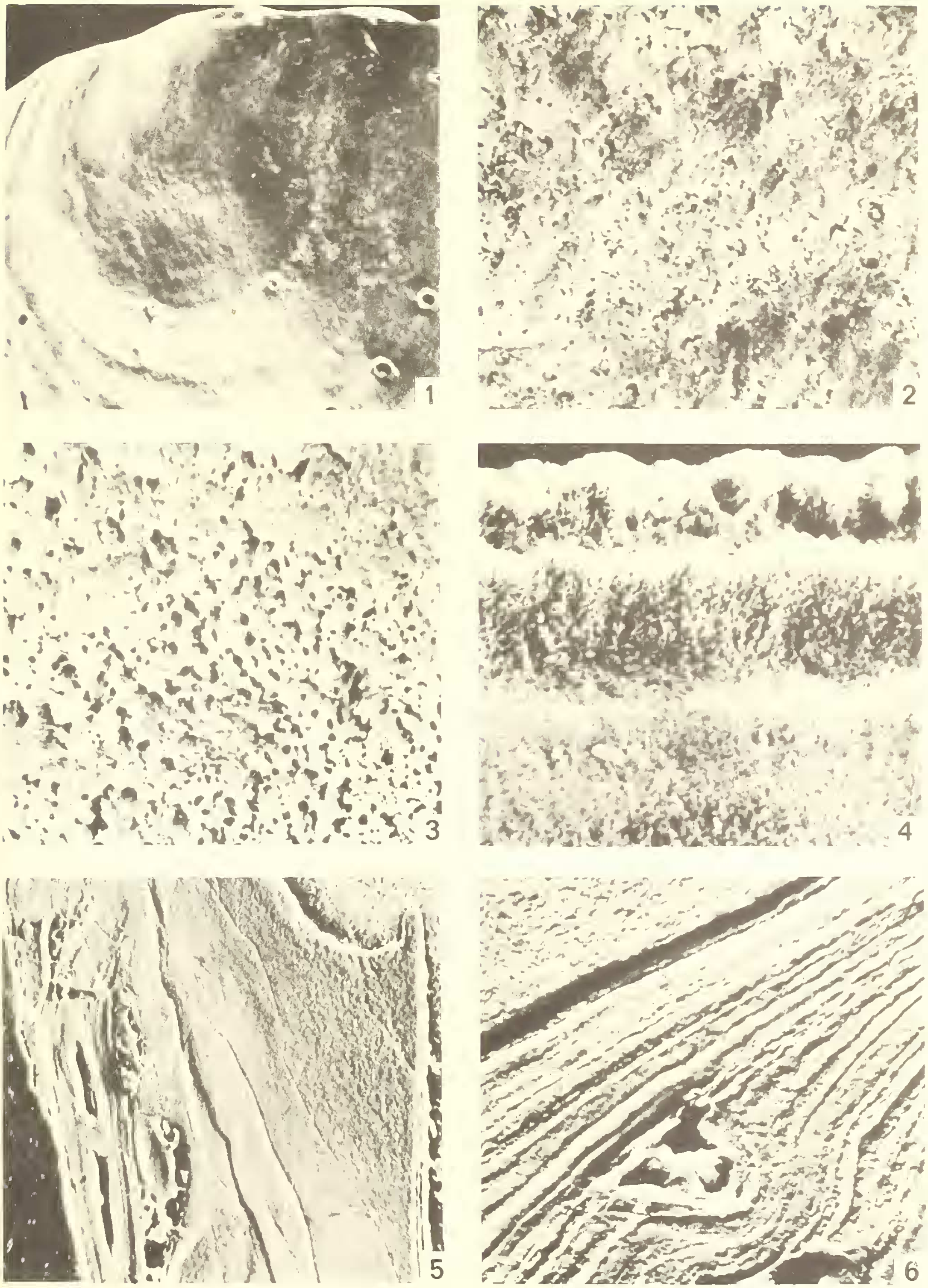
EXPLANATION OF PLATE 75

Figs. 1–6. Scanning electron micrographs. 1. Umbonal region of brachial valve of *Helmersenia ladogensis* to show the extent of the protegulum and the restriction of spines to the post-protegular part of the valve (×120). 2–3. Details of protegular surfaces of brachial valves of *Multispinula perspinosa* and *Siphonotreta verrucosa* respectively showing solution pits (×2800). 4. Detail of oblique fracture surface through brachial valve of *Siphonotreta unguiculata* showing layers of apatite crystallites; exterior towards top of micrograph (×2200). 5. Differentially etched section of brachial valve of *Siphonotreta verrucosa* showing origin of small spines to left and internal blade-like projection in top right; anterior of valve to bottom of micrograph (×250). 6. Differentially etched section of brachial valve of *Siphonotreta unguiculata* showing banding; exterior at top left hand corner of micrograph (×1200).



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more than 400 nm thick in *Helmersenia*. The skeletal ultrastructure of living Acrotretida suggests that these layers represent extensive laminae of apatite separated from one another by residues of the chitino-proteinaceous sheets on which the apatite crystallites were originally deposited. The distribution of solution pits and their disposition more or less normal to the protegular surface further suggests that the crystallites were secreted with their long axes vertical to the chitino-proteinaceous sheets.

The fact that the surface of the siphonotretacean protegulum is smooth in its unweathered state indicates that the inner sealing membrane of the periostracum, which acted as a seeding sheet for the outermost mineral layer of the shell, was also featureless. Thus the periostracum itself may have been a homogeneous mucopolysaccharide layer as in living craniceans, or a vesicular layer with a thick inner sealing membrane as inferred for the adult acrotretacean shell.

THE ADULT SHELL

The siphonotretacean adult shell is structurally similar to that of other chitinophosphatic inarticulate brachiopods. The ultrastructure is best studied in oblique natural fractures (Pl. 75, fig. 4) and prepared sections (Pl. 75, fig. 6) of the relatively thick shell of *Siphonotreta unguiculata*; and the arrangement seen in that species is typical of other siphonotretacean stocks. The shell is finely layered with 15 bands having an average thickness of 1 μm. The commonest type of band is made up of fine crystallites rarely more than 500 nm across. It has not been possible to decide whether the crystallites are epitaxially arranged from one band to the next. In any event it is likely that the banding, as in the protegulum, represents apatitic laminae that were originally separated from one another by chitino-proteinaceous sheets. Indeed, oblique fractures commonly show groups of 2–5 closely spaced bands with surfaces that are homogeneous at the resolutions possible with a scanning electron microscope. These bands are probably composed mainly of proteinaceous derivatives and would have been deposited during periodic changes in the secretory regime of the *Siphonotreta* mantle.

In *Siphonotreta* and *Multispinula*, narrow strips of shell, as interwoven lines with angular junctions, usually occur on the shell exteriors anastomosing around spinal bases (see bottom left-hand corner Pl. 76, fig. 2). Each strip has a slightly undercut edge so that it forms an overlapping film of shell about 1 μm wide. In living articulate brachiopods, the shell surface immediately beneath the periostracum may bear furrows or ridges which are presumably mineral casts either reflecting inequalities in the inner surface of the periostracum, or coinciding with intercellular boundaries. Polygonal areas enclosed by the strips on siphonotretacean shell surfaces are too large to represent cell outlines. Provisionally, they are interpreted as having been secreted within microscopic folds in the seeding surface of the periostracum.

In *Helmersenia* but especially in *Multispinula* and *Siphonotreta*, concentric lamellae, up to 150 μm long, regularly occur. The last two genera are also characterized both externally and internally by raised concentric ridges (Pl. 76, figs. 1, 5). In *Multispinula* they occur externally as more or less continuous asymmetrical ridges at intervals of about 150 μm in the middle regions of the shell with the steeper side facing anteriorly. In *Siphonotreta*, similarly disposed asymmetrical ridges, about 20 μm high, occur. These tend to be impersistent over the immature shell surface but are more continuous and more widely spaced, at intervals of about 300 μm, in the adult shell. In both genera, internal concentric features occur at intervals of 500–700 μm as blade-like projections extending posteriorly for about 30 μm (Pl. 75, fig. 5). In no species, however, is any ornamentation so conspicuous as the prostrate spines distributed in different patterns over the surface of the adult shell.

Distribution of spines. The spines arc restricted to the post-protegular part of the adult shell where they form dense arrays as defined by Rudwick (1965, p. 605). The simplest array is found in *Helmersenia ladogensis.* In this species, the spine bases, which are distributed alternately and radially at intervals of about 100–200 μm, must have borne spines of only one size grade. The bases are usually oval in outline with their major diameters, averaging about 45 μm, aligned radially (Pl. 76, fig. 3) and frequently coincident with slightly raised ridges trailing off for a few micrometres on either side. Although no spines have been seen it is evident, from the slope of fracture surfaces defining their bases, that they must have lain sub-parallel, or at a small angle, to the shell surface (compare the rare remnants of spines in *H. ladogensis* figured by Goryansky 1969, pl. 19, figs. 1 and 2). Each spine base communicates with the shell interior by a central canal, about 10 μm in diameter, which is disposed normal to the surface of the valve.

The arrays found in *Siphonotreta* and *Multispinula* are more complicated because they involve two sets of spines as already noted by Cooper (1956, p. 268) in his study of the latter genus. These sets can be distinguished by differences in their structural relationship to the shell as well as in their mean diameters (cf. Pl. 76, figs. 1, 5). The average lengths of the sets must also differ significantly, although both kinds of spines have been broken off the shell near their bases and no reliable estimates were obtained during this study. Some indication, however, can be given of the minimum length of the spines; in *Multispinula*, for example, the larger spines are at least 6 mm long (Cooper 1956, p. 268) and the smaller ones 1·3 mm according to our investigations. Presumably a comparable order of difference is characteristic of the two spine sets developed in other siphonotretacean species.

In *Siphonotreta verrucosa*, a set of larger spines, which correspond to those of *Helmersenia*, occurs radially and alternately at about 1 mm intervals (Pl. 76, figs. 1, 2). These external spines are subcircular in section near their bases where they average 220 μm in diameter for 4 estimates. Each is pierced by a central canal with an average diameter of 80 μm. The canal runs obliquely through the valve to communicate with the shell interior by an inwardly directed spine which is up to 360 μm long and tapers to a diameter of about 50 μm. The internal spines (Pl. 76, fig. 4) are usually fluted longitudinally at

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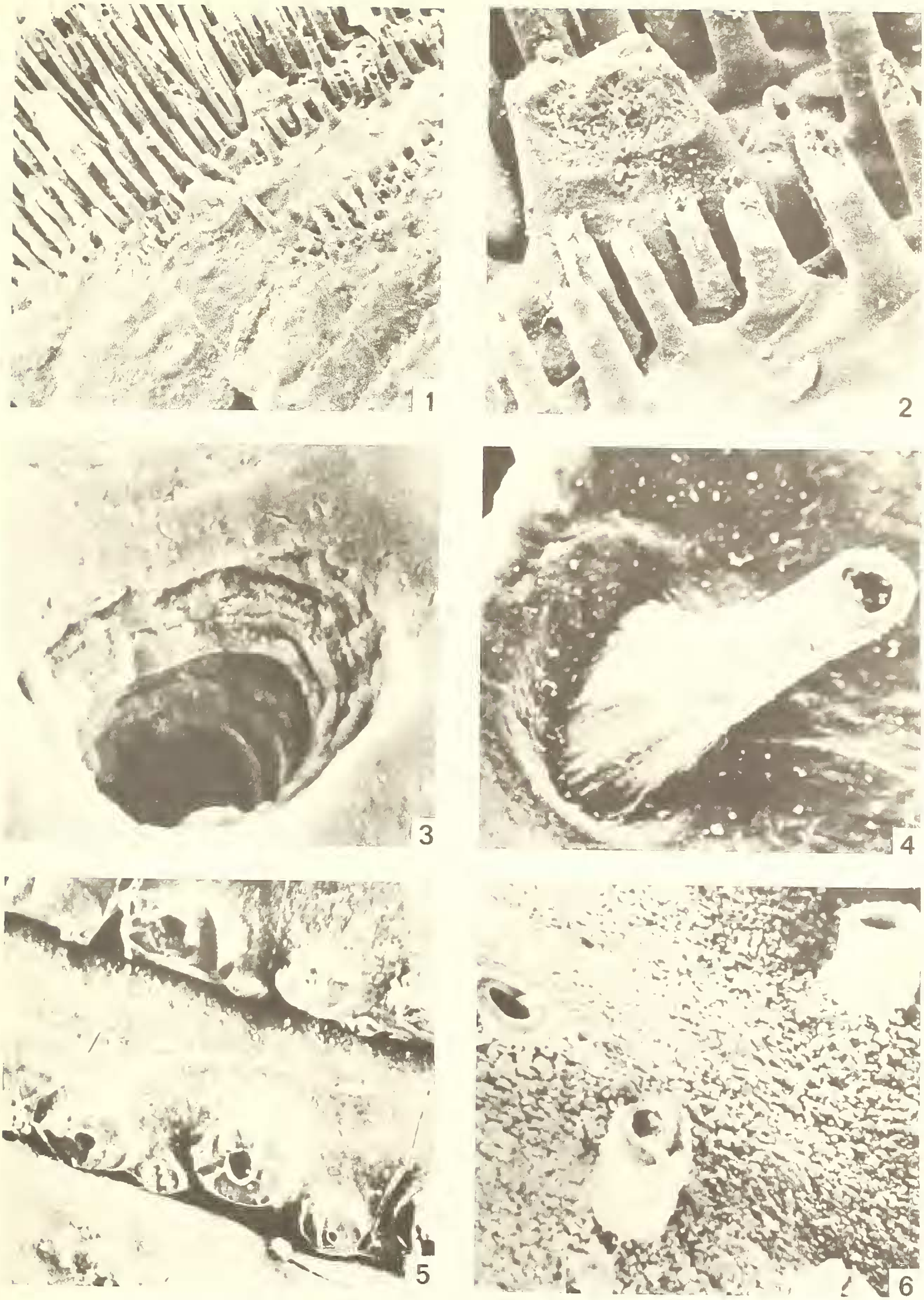
EXPLANATION OF PLATE 76

Figs. 1–6. Scanning electron micrographs. 1–2. Exterior near antero-lateral margin of brachial valve of *Siphonotreta verrucosa* to show two sets of spines; valve margin beyond top left hand corner (×30, ×150). 3. Exterior of brachial valve of *Helmersenia ladogensis* with spine broken off at base to show canal piercing shell (×2400). 4. Interior of brachial valve of *Siphonotreta verrucosa* showing internal extension of a large spine (×300). 5. Exterior near antero-medial margin of brachial valve of *Multispinula perspinosa* showing two sets of spines; valve margin beyond bottom left hand corner (×120). 6. Interior of brachial valve of *Multispinula perspinosa* showing internal extensions of large spines (×575).



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